CHRYSOPHYTE BLOOMS IN THE PLANKTON AND NEUSTON OF MARINE AND FRESHWATER SYSTEMS

AUGUST 1992

Ontario
Environment
Environnement

ISBN 0-7729-9997-X

CHRYSOPHYTE BLOOMS IN THE PLANKTON AND NEUSTON OF MARINE AND FRESHWATER SYSTEMS

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AUGUST 1992

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PIBS 2082
Log 92-2345-107

ABSTRACT

This report reviews the major developments in recent understanding of bloom-causing chrysophytes in both marine and freshwater environments. It also points out information deficiencies and suggests lines of future research.

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INTRODUCTION

Excessive accumulations of algae in freshwater lakes and coastal marine environments have been observed for centuries. Homer's *Illiad* mentions discolouration of the sea and the Bible contains a reference to "the bloodied waters of the Nile". Charles Darwin apparently observed a "red tide" off the coast of Chile, and North American Indians wouldn't eat shellfish from "shining waters" based on previous experiences with algal bloom related shellfish poisonings (Red Tide Newsletter 3(2), April 1990). Among the causes most often cited are enrichment of aquatic systems with nutrients from human activities (Vallentyne, 1974; Smayda and White, 1990). While there is strong evidence that excessive supply of nitrogen and phosphorus and other nutrients is often the underlying cause of algal blooms, it is also clear that bloom development depends upon the coming together, in appropriate combination, of a number of critical biotic, physical and chemical environmental factors (Paerl 1988).

The implication of the early historical evidence of algal blooms is that the consequences of accelerated human population growth and contemporary urbanization and industrialization activities cannot be the only causative factors for algal blooms. For example, there were especially intense blooms of the dinoflagellate Alexandrium cantenella off the Norwegian coast in 1988, which may have been in response to abnormally high water temperatures. Paleo-oceanographic evidence (B. Dale, University

of Oslo, unpublished) suggests that similar blooms developed as far back as 2000 years ago when human induced influences were undoubtedly negligible.

During the past 5-10 years, however, there is good evidence that the frequency, intensity and geographic extent of algal blooms, in both freshwater (Skulberg et al. 1984) and marine environments (Smayda 1990), have increased dramatically in response to human influences related mainly to active transport of bloom-causing organisms (e.g., ship ballast, aquaculture stocking) and stimulation of bloom development by nutrient enrichment. Until recently, the algal bloom phenomenon was generally believed to be monopolized by blue-green algae in lakes and dinoflagellates in the sea, although less significant blooms caused by other algal groups have been recognized (Pearl 1988). The International Conference on Toxic Dinoflagellates (1974, 1978, 1985) changed its name for the June 1989 meetings in Sweden to "The Fourth International Conference on Toxic Marine Phytoplankton" in order to better reflect the recent catastrophic non-dinoflagellate blooms of the mid- to late 1980s. These blooms resulted in human death and sickness, severe economic losses and inestimable ecological damage and were caused by the prymnesiophytes Chrysochromulina polylepis and Prymnesium parvum in Scandinavian coastal waters in 1988 and 1989 (Underdal et al. 1989; Kaartvedt et al. 1991), the chrysophyte Aureococcus anophagefferens in New England in 1985-1988 (Nuzzi and Waters 1989; Cosper et al. 1990), and the diatom Nitzschia pungens f. multiseries on Canada's east coast in 1987 (Subba Rao et al. 1988). In freshwater, algal blooms of non blue-green origin with economic and/or nuisance/aesthetic implications,

have included the dinoflagellates Ceratium hirundinella (Nicholls et al. 1980) and Glenodinium sanguineum (Dodge et al. 1987), the prymnesiophyte Chrysochromulina breviturrita (Nicholls et al. 1982) and the chrysophytes Synura petersenii (Nicholls and Gerrath 1985), Synura uvella (Clasen and Bernhardt 1982) and Uroglena americana (Kurata 1989). These species are only the tip of the iceberg however; a recently published guide to the taxonomy of organisms causing "red tides" in Japan (Fukuyo et al. 1990) includes 200 species representing ten algal classes. Interestingly, this comprehensive listing includes only one chrysophyte species (Uroglena americana).

It is clear, therefore, that with so many different taxa now implicated in algal blooms, bloom phenomena present special challenges to both the scientist and the user of aquatic resources concerned about understanding and predicting the potential for bloom development and toxin production. This paper reviews the major developments in recent understanding, as well as the major information deficiencies relating to bloom-causing chrysophytes in both marine and freshwater environments.

Bloom Definition

Phytoplankton blooms have been defined in different ways (Pearl 1988; Richardson 1989; Legendre 1990). For the purposes of this paper, I define a chrysophyte bloom as an accumulation of organisms of the classes Chrysophyceae and/or Synurophyceae to a level of intensity which results in one or more of the following:

1) a visible colouration of the water,

2) an effect on aesthetic value and/or human use of the water (e.g., taste and odour problems in water supplies),

3) major direct effects on other aquatic biota (toxin production, physical damage, e.g., clogging of gill lamellae), and

4) major indirect effects on other biota (e.g., food web disruption leading to starvation, dissolved oxygen depletion resulting from bloom decomposition).

Marine Chrysophyte Blooms

The most important species of marine chrysophyte causing blooms (and the only species discussed in this paper) is Aureococcus anophagefferens, a picoplanktonic alga, first described by Sieburth et al. (1988). This species, which may be synonymous with the open ocean taxon Pelagococcus subviridis (Cosper et al. 1990), developed dense blooms in embayments of Long Island, New York in 1985-1988 and quickly gained notoriety as "brown tide" throughout the region including parts of New Jersey and Rhode Island Sound where it was also observed (Nuzzi 1988; Nuzzi and Waters 1989; Smayda and Villareal 1989). After the initial invasion in 1985, the brown tide did not return to Naragansett Bay in 1986, but did to Barnegat Bay and to the Long Island bays during three subsequent years, but at lower densities. Densities during the peak of the 1985 bloom approached 3×10^9 cells/L.

The effects of the Aureococcus blooms were disastrous. Anecdotal evidence suggested that thousands of acres of eelgrass (Zostera marina) beds, plants which are important as settling sites for larval shellfish, were essentially eliminated through light exclusion effects (Nuzzi 1988); however, quantitative data on distribution and density immediately before and after the bloom years apparently does not exist (Dennison et al. 1989). Because the critical life history of the bay scallop (Argopecten irradians) through larval, immature and sexually mature adult stages covers less than a two year period, the bay scallop fishery was virtually wiped out (Bricelj and Kuenstner 1989) where the Aureococcus bloom developed during two consecutive years. The effect was one of physical interference in filter feeding so that the scallops apparently starved to death; no toxicity has been implicated (Gallager et al. 1989; Ward and Targett 1989). The combined value of the annual bay scallop, blue mussel and cultured oyster (Crassostrea virginica) harvest from this region, lost to the effects of the brown tide, was over $2.5 Million (Nuzzi 1988). Other damage was not easily quantified. For example, terns and other fish-eating birds left the region apparently because they couldn't see their prey (Nuzzi 1988).

The critical questions at the time of the Aureococcus bloom were obviously related to the cause. Why did it happen? First of all, it is unfortunate that it seemed to take a catastrophic event like this to focus attention on a chrysophyte. One major consequence of this bloom was that there followed a flurry of research activity at laboratories in the region. Aureococcus was brought into laboratory culture from isolations made in 1986

and effects on growth rates of several environmental factors were determined. Field studies to determine the water quality /productivity relationships in Long Island Sound area were also initiated (Nuzzi and Waters 1989; Cosper et al. 1989). Cosper et al. (1987) showed that Aureococcus grew much better in enriched coastal bay water than in enriched synthetic ocean media. Dzurica et al. (1989) achieved improved growth of Aureococcus in media containing organic phosphate compounds auch as glycerophosphate and chelating agents such as nitrilotriacetic acid (NTA) and citric acid. This species also demonstrated strong heterotrophic growth capabilities with rapid uptake of glutamic acid and glucose. Still, the culture studies alone were not able to link these special characteristics of laboratory growth to bloom development..."How these factors are involved in the dominance of A. anophagefferens over other phytoplankton species in nature remains to be further investigated..." (Dzurica at al. 1989).

One of the most convincing explanations for the cause of the bloom was developed by Cosper et al. (1990). I have summarized it here, because it appears to represent a particularly good example of the fortuitous interaction of a number of environmental factors with the particular physiological adaptations and requirements of Aureococcus. It is an attempt to communicate more widely the Cosper et al. hypothesis in the hope that it might serve as a model for explanations of other algal bloom phenomena, possibly involving multiple environmental factors.

The first important point to realize is that the brown tide occurrence in 1985 was over a wide geographic area, and because the bloom did not appear to spread from one coastal bay system to the next, but rather developed more or less simultaneously at all locations, factors initiating the bloom appear to be regional (e.g., weather) rather than localized (e.g., the effects of a single point-source of nutrients). In this regard, the precipitation data are most revealing. Rainfall on Long Island during 1985 was the third lowest since 1949 and was again well below the annual average in 1986 and 1987. This low precipitation resulted in salinity levels that were 20% higher than normal. The laboratory studies had shown a severe reduction in growth rate of Aureococcus below 28 ppt, compared with 30 ppt, but growth at the lower salinities could be enhanced by addition of organic rather than inorganic nutrients. This is where the seasonal pattern of annual precipitation is apparently of some importance in bloom development. Aureococcus blooms developed during the summers of 1985, 1986 and 1987, but were most intense in 1985 and least intense in 1987. During 1985 and 1986, low winter rainfall was followed by high precipitation in spring. In 1987, spring precipitation was low and the bloom was not nearly as well developed. The implication is that rainfall was important for nutrient supply, but only enhanced bloom development if it followed a period of low rainfall which set up the optimum salinity levels. In addition, the low winter rainfall resulted in generally longer water residence times in the Long Island Sound embayments thereby helping to ensure that an adequate overwintering "seed" population was present for the summer season (Fig. 1).

The Cosper et al. explanation for the Aureococcus bloom might be expanded after further investigation to include some additional facts and suggestions put forward by Sieburth (1989) and Minei (1989) relating to the possible stimulatory effects of agricultural and lawn fertilizers on Aureococcus and toxic effects of pesticides on zooplankton in the Long Island area.

Freshwater Chrysophyte Blooms

Phytoplankton

A number of chrysophyte taxa are known to produce substantial populations in freshwater lakes and ponds. These include Mallomonas acaroides, M. caudata and M. crassisquama (Kristiansen 1971; Thomasson 1970), Chrysosphaerella longispina (Pick et al. 1984), several Dinobryon species (Eloranta 1989), Uroglena americana (Kurata 1989), Synura spp (Nicholls and Gerrath 1985; Clasen and Bernhardt 1982). In this review, I will restrict my summary to those genera known for their production of odour and associated problems in domestic water supplies, recreational lakes and reservoirs.

Odours from blooms of Dinobryon, Synura, and Uroglena have most often been described as fishy, but other descriptors include "cod liver oil" and "muskmelon" or "cucumber", especially for the early bloom stages of Synura (Whipple et al. 1948; Lackey 1950; Palmer 1962; Taft 1965).

Where surface waters provide the raw water source for municipalities, some level of treatment is usually provided before distribution to consumers. This treatment can range from simple disinfection to complex filtration/sedimentation procedures. Excessive densities of algae in the influents to these water treatment plants disrupt their normal functioning and usually require modifications to routine operations including more frequent filter backwashing, installation of microstrainers, adjustments to chemical flocculation routines, or more expensive activated carbon filtration (Hutson et al. 1987). At locations where only limited treatment is provided, as for example in regions of chronic economic depression or where the source water supply has historically been of good quality, occasional algal blooms may impart off-flavours which get through the system to the consumer. At such times, complaints from consumers to water treatment operators and waterworks officials are usually described by reference to common naturally occurring odours, such as musty, earthy, fishy, oily, geranium, septic, etc. The general practice of water treatment personnel is at least to record any complaints from consumers and charactize the type of odour (Table 1). There is of course a danger in assuming that all "fishy" odours in water supplies arise from chrysophyte blooms because fish-like odours can originate from the decomposition of certain protein complexes. Only rarely have chemical analyses been undertaken to characterize precisely the odour causing compounds (Mallevialle and Suffet 1987).

A more ideal situation results from microscopic identification of organisms in the raw (untreated) water source at the first sign of an odour problem (e.g., Table 2). One

difficulty with this scenario is that the odour from an algal population may not arise until near the end of its period of healthy growth. So, by the time it is recognized as a problem and investigated, some other species may have assumed dominance in the phytoplankton. The result is that some "innocent" species may be mistakenly identified as the problem organism (Fig. 2). Clearly, quick reaction times between odour detection and identification of the cause are necessary to avoid erroneous explanations.

At some water treatment plants, the need for timely and accurate diagnosis has led to the establishment of regular phytoplankton monitoring and routine measurements of threshold odour concentrations (APHA 1985; Persson 1983; Persson and Jüttner 1983). The data thus obtained permit the judicial application of remedial measures such as activated carbon filtration in a cost effective, short-term, proactive manner.

Because chrysophytes tend to dominate the phytoplankton of north-temperate, oligotrophic lakes (Janus and Duthie 1979; Eloranta 1986, this volume; Earle et al. 1986; Willén et al. 1990; Pinel-Alloul et al. 1990; Nicholls et al. 1992), the major human use of such lakes is for recreational purposes, rather than for drinking water supplies. However, as was the case with drinking water supplies, the best source of information about chrysophyte related odour problems may originate from user complaints.

In Ontario during the past four years, we have been made aware (through user complaints) of nine episodes of fish-like odour production by Uroglena blooms. These

nine lakes (Table 3) included a wide range of lake type, from shallow, dystrophic lakes such as Black Lake, to deep, clear water lakes such as Kawagama Lake. It is clear, therefore, that circumstances other than nutrient supply alone are responsible for such blooms. The species of Uroglena causing blooms in Ontario lakes have not been determined, but in the case of perhaps the best known Uroglena lake in the world, Lake Biwa in Japan, considerable research has been undertaken to determine the factors stimulating growth and causing of recurrent blooms of U. americana since the early 1970s (Yoshida et al. 1983a, 1983b, 1983c; Kimura and Ishida 1986; Kimura et al. 1986; Kurata 1986, 1989).

Taste and odour problems in Ontario lakes that originate from Synura have been more widespread than those induced by Uroglena. Some of these episodes were reviewed by Nicholls and Gerrath (1985) and it was concluded that in every case, in both hardwater and softwater lakes, only one of the 20 known species of Synura (S. petersenii) was the cause.

Characterization of Chrysophyte Volatilities

There have been only two or three significant studies of the volatile excretory products of chrysophytes. Collins and Kalnins (1965) reproduced typical Synura odours in the laboratory in bacteria-free cultures. By applying their solvent extraction and thin layer chromatographic methods to culture filtrate as well as directly to cell concentrates, they

showed that the odour causing compounds were aldehydes and ketones (mainly n-hapanal), which were excreted by living cells into the growth medium.

Some further work on a Synura bloom occurring in the Wahnbach Reservoir in Germany was reported by Jüttner (1981, 1983), and based on similar findings from cultures of two Ochromonas species, it was concluded that the Chrysophyceae, like higher terrestrial plants, produce a wide spectrum of volatile organic compounds including a number of dienals, alkenols, alkenones, alcohols and ketones (Table 4), of which oct-1-en-3-ol, pentanone-3 and octanone-3 were the most important. Yano et al. (1988) identified the related compounds (E,E)-2,4-heptadienal and (E,Z)-2,4-heptadienal as the causes of the fishy odour in a Uroglena bloom in the Ninobiki Reservoir in Japan.

Bloom Development - Ecological Considerations

Aside from the explanation offered for the Aureococcus bloom, I have not to this point discussed chrysophyte bloom ecology. The risk in delving into this topic is that I would be repeating much of the information presented by other contributors to this volume under the related topics of chrysophyte distribution, ecology and paleoecology. This is because many of the strategies that permit chrysophytes to survive and flourish in lakes are undoubtedly related to similar factors involved in bloom development (see also review by Sandgren 1988). Therefore, this section on chrysophyte bloom initiation will include only the essential highlights of the ecology of bloom-forming species, so that

more space can be devoted to detailing what I consider to be the major deficiencies in our understanding of the chrysophyte bloom phenomenon. Hopefully, this approach will provide some direction for future research and management.

An understanding of the ecology of bloom forming chrysophytes must be based on a solid physiological foundation. A classic example of this is the historical development (spanning a period of nearly half a century) of the understanding of the relative roles of phosphorus and potassium as factors controlling Dinobryon populations (see Shapiro 1988, p.11). Quantitative ecophysiological investigations of the bloom-forming Chrysophyceae probably had their beginnings with the work of Gaidukov (1900) who determined that Chromophyton rosanoffii Woronin emend. Couté (Gaidukov's "Chromulina rosanoffii") could be grown in a defined mineral medium. Subsequently, Guseva (1935) was able to examine growth rates of Synura uvella and S. petersenii in cultures based on isolations from the Moscow River Oxbow and from some peat pits in the vicinity of Bolshero. She discovered that iron concentrations were critical for good growth in both species. Optimum iron concentrations of 1.2-1.4 mg/L and nitrogen concentrations of 1.0-2.0 mg NO_3^--N/L and 0.1-0.2 mg NH_4^+-N/L were determined for S. petersenii. Today, we know that the relatively high iron requirement by Synura species relates to their use of iron-containing cytochrome-C as an electron donor in photosystem-I (Raven, this issue). The tendency for certain Synura species to develop large populations in dystrophic lakes and ponds may depend, in part, on the availability of iron. Dokulil and Skolaut (1991) concluded that the summer populations of Dinobryon

species in the Mondsee in Austria were dependent on the supply of iron, the availability of which was controlled through chelation by organic substances released by decomposition of the spring diatom populations.

Light may also be a factor controlling bloom development in dystrophic waters, owing to its rapid attenuation by dissolved organic matter (Jones and Arvola 1984). Little is known, however, of the light quality and quantity preferences and the physiological adaptive responses by phytoplankton as a whole (Falkowski 1984), let alone chrysophytes in particular. In experiments on the role of colour and light intensity on the distribution of several phytoplankton species, Wall and Briand (1979) found that chrysophytes represented by Dinobryon and Mallomonas species tended to be favoured more by blue light than were other groups of algae. They suggested that this is consistent with the known vertical distribution of these algae in lakes and that the deep water occurrence of these species may indicate a competitive advantage over other algae better suited to use the higher intensity red wavelengths in surface waters.

There is ample evidence of stratified subsurface chrysophyte populations in lakes (Fee 1976; Nygaard 1977; Pick et al. 1984; Croome and Tyler 1988) and diurnal migrations of some taxa have been demonstrated (Ilmavirta 1974; Jones 1988). The most obvious attribute that the presence of flagella has provided to each of the genera being discussed here (Dinobryon, Synura, Uroglena and Mallomonas) is the ability to "swim". Subsurface populations of these organisms are clearly there by choice. The suggestion above was

that some relative advantage over other algae relating to light quality and intensity may exist for these motile chrysophytes. The operative word is "relative" because laboratory studies have shown that species achieving significant populations in the wild at low light and temperature may grow equally well or better at higher light intensities and higher temperatures in the laboratory. For example, Healey (1983) showed that growth rate of Synura sphagnicola isolated from a submetalimnetic bloom (ambient light 1% of surface irradiance and temperature = 7-8° C) was a saturable function of light intensity over a temperature range of 5-20° C in the laboratory (Fig. 3).

If light and temperature are not optimal for these organisms at these depths, then they must be actively seeking these strata out for other reasons. Nutrient concentrations are usually higher within and below the metalimnion because of decomposition and mineralization of materials sedimenting from the upper trophogenic zone combined with the upward diffusion of dissolved matter released from the lake sediment and/or from similar processes of decomposition in the hypolimnion. By virtue of its motility, a cell in a homogeneous solution of dissolved nutrients is ensuring a constant and maximum concentration gradient across the cell membrane (assuming constant uptake rate and constant swimming speed). While it has been shown that the net energy gain to a motile cell (compared to a non-motile cell) under these conditions is negligible (Sommer 1988), there may be considerable advantage in expending energy to seek out and remain in strata with higher concentrations of essential nutrients. Bloom-forming species of Mallomonas, Dinobryon, Synura and Uroglena are all large and highly motile. One

advantage that taxa with the ability to move vertically in the water column may have over those that do not is exposure to "pockets" with higher nutrient levels; they are thus able to exploit heterogeneities in growth promoting substances in their environment within the limits of their swimming capabilities and net energy expenditures.

Biotic and Anthropogenic Factors

In general, chrysophytes tend to comprise a significant proportion of the total phytoplankton of oligotrophic to mesotrophic lakes. The role of nutrients, originating from human activities, as triggers of chrysophyte blooms is not clear, although it is evident that substantial populations may develop in lakes and ponds with significant inputs of nutrients. In eutrophic lakes, the seasonal distribution of chrysophytes may be restricted mainly to early spring (Kristiansen 1988). Munch (1972) and Roijackers (1985) both reported occasional blooms of Synura or Mallomonas in productive dimictic lakes. Generally, eutrophied lakes are poorly represented by chrysophytes, but when point-source nutrient loading controls have been initiated, the relative importance of chrysophytes has increased (Dillon et al. 1978; Nicholls et al. 1986; Willén 1987). Conversely, fertilization of low-productivity lakes has sometimes been followed by blooms of chrysophytes, but the results thus far have not been consistent (Table 5). For example, Langford (1950) fertilized four lakes in Ontario with a 12-24-12 formulation of a commercially available fertilizer and achieved epilimnetic concentrations of total P ranging from 0.05 to 0.9 mg/L (as P). All lakes, except an unfertilized control lake,

responded to treatments 3-4 weeks later with increases in Tabellaria, Asterionella and Dinobryon. One of the lakes produced much higher densities of Synura. In contrast, Lake Langvatn in central Norway showed no response among Synura, Uroglena, or Dinobryon at fertilizer application rates similar to those used by Langford (Reinertsen 1982). In northern Sweden, a Uroglena bloom resulted from fertilization with nitrogen alone in one lake, but no bloom developed in another lake receiving a similar treatment (Holmgren 1984).

The responses of Dinobyron to lake fertilization are interesting. The early belief that phosphate was toxic to Dinobryon, even at relatively low concentrations, was challenged by Lehman (1976), who showed that when phosphorus was supplied even at high concentrations to Dinobryon cultures as K_2HPO_4 or KH_2PO_4, potassium, not phosphorus, was the toxic element. However Lehman's work showed inhibition of growth of D. sociale var. americanum and D. cylindricum at K concentrations greater than 500 μg/L and 7500 μg/L, respectively, and these results do not entirely explain the inhibition observed by Rodhe (1948) at much lower concentrations of K (25 μg/L). More recently, Wilcox and DeCosta (1984) also observed a rapid disappearance of Dinobryon in experimental enclosures fertilized with KH_2PO_4 (100 μg K/L). Holmgren (1984) found an apparent inhibition of Dinobryon spp. in a lake fertilized with phosphate alone (as H_3PO_4), but Dinobryon spp. were consistently among the dominants in Lake ELA 261 after fertilization with H_3PO_4 (Table 5). Clearly, the role of nutrient supply in chrysophyte bloom development is poorly understood, but it is possible that in

combination with other factors, small increases in nutrient supply are stimulatory to some chrysophyte populations.

Factors contributing to chrysophyte blooms probably relate as much to strategies that allow populations to avoid losses as to factors that contribute directly to optimum growth. Another advantage of the capability for vertical movement in lakes may be that it affords protection from zooplankton grazing. In laboratory studies, Sandgren (this issue) has demonstrated that Synura and other large chrysophytes are utilized as food items by large Daphnia species, presumably through consumption of individual cells rather than whole colonies. In support of these findings, Sandgren (ibid) assembled data from the literature which showed that the presence of populations of large Daphnia in lakes was associated with depressed chrysophyte populations. This finding raises an interesting "chicken and egg" question: Is the predominance of chrysophytes in softwater lakes a direct physiological response to chemical characterists of low pH waters, or is it in response to decreased Daphnia grazing, since Keller et al. (1990) have shown with field data and laboratory bioassays that densities of Daphnia galeata mendotae decline in lakes below pH 6.0? Sandgren concluded that there is no refuge from zooplankton grazing by virtue of large size among chrysophytes. There may, however, be protection afforded by the deeper portions of the vertical migratory route (metalimnion or upper hypolimnion) where low water temperatures are associated with low metabolic rates of the grazing animals at these depths.

In summary, large populations of chrysophyte species may develop in softwater lakes because of their ability to grow well at low temperatures and low light intensities (although these may not be optimal), combined with the minimization of zooplankton grazing impacts and adequate nutrient supplies. The latter two factors may be augmented by human influences. For example, removal of large piscivorous fish results in enhanced zooplanktivore populations and increased predation on large zooplankton species. Watershed deforestation, human wastewater seepage and agriculturalization all result in increased nutrient inputs to lakes, and the effects of acid deposition may act as a double edged sword: 1) by decreasing lakewater alkalinity and thereby putting additional stress on Daphnia spp., and 2) by enhancing leaching of growth promoting substances (including trace metals such as cobalt needed for subsequent synthesis of vitamin B_{12}). The combined effects of eutrophication and acidification have been blamed for the recent algal blooms in Scandinavian coastal waters (Sangfors 1988; Granéli et al. 1989).

While these factors may explain the occurrence of large chrysophyte populations (Fig. 4), they do not necessarily explain some aspects of the bloom phenomenon itself. For example, Uroglena blooms are often manifested as sudden mass accumulations at the lake surface, much like the blue-green algal bloom phenomenon. Unlike the blue-green algal bloom, for which an ecophysiological explanation exists (Reynolds and Walsby 1975), no similar explanation for the sudden surface accumulation of Uroglena has been suggested. Considerable laboratory study of the now common Lake Biwa Uroglena

blooms has contributed much to an understanding of phagotrophism, nutrient, trace metal and vitamin requirements (Yoshida et al. 1983a, 1983b, 1983c; Kimura and Ishida 1986; Kimura et al. 1986; Kurata 1986, 1989). The apparently now common episodes of Uroglena surface blooms in Ontario (Table 3), may afford additional opportunities to determine the factors contributing to the surface accumulations.

Neuston

The term "neuston" was first used by Naumann (1917) to designate the community of organisms associated with the surface microlayer of lakes and ponds. Its use in freshwater and marine contexts has been reviewed by Banse (1975) with reference to subdivisions of the neuston (e.g., epineuston, hyponeuston) and other "nearby" biotopes in aquatic ecosystems. It is important to realize that organisms inhabiting the neuston are there for reasons related to surface tension, not because of buoyancy adaptations; so, by definition, the neuston excludes surface accumulations of gas vacuolate blue-green algae.

The neuston communities of freshwaters may include a wide variety of taxa (Frølund 1977; Fuhs 1982a, 1982b; Pentecost 1984; Estep and Remsen 1984; Timpano and Pfiester 1985). The highly visible oily sheen produced on the water surface by several chrysophytes qualifies this type of growth as a "bloom" under the definition used in this paper. The most commonly reported neustonic chrysophyte is Chromophyton rosanoffii

Woronin emend. Couté (Couté 1983), which forms curious epineustic "pseudocysts". Some aspects of the life history and seasonal development of this species have been presented by Petersen and Hansen (1958) and Frølund (1977) who found a maximum density of about 2 X 10^6 cells /cm^2. Heynig (1972) has also included C. rosanoffii among a listing of other freshwater bloom forming algae such Aphanizomenon, Microcystis, Dinobryon, Ceratium and Botryococcus.

Other Chrysophyceae known to inhabit the neuston (but not necessarily excluded from planktonic, benthic or epiphytic existences in other habitats) include Chromulina neustophila Conrad (Conrad 1940), Paraphysomonas vestita (Stokes) de Saed. (Frølund 1977), Epipyxis minuta (Mack) Hilliard (Petersen and Hansen 1958 [as Hyalobryon minutum Mack]), Hyalocylix stipitata Pet.& Han. (Petersen and Hansen 1958), and Kremastochrysis minor Catalan (Catalan 1987). Two or three other Chromulina species are probably synonymous with Chromophyton rosanoffii since cell habit and morphology appear identical except for the likely omission of the second short flagellum (Couté 1983). Those neustonic chrysophytes forming visible blooms are likely restricted to C. rosanoffii, C. neustophila and K. minor.

The surface microlayer may also be enriched with bacteria (Maki and Remsen 1989). Because chrysophytes of the Ochromonas-type are known facultative phagotrophs, the generally low light environment of woodland ponds might provide a competitive advantage to such chrysophytes as Chromophyton over other algae which must depend

only on autotrophic nutrition under conditions of higher light than is generally available in shaded forest pools, which seem to be the preferred habitat of Chromophyton. Once established in the neuston with some dependence on bacteria for a portion of their energy supplies, other variables might enhance the availability of nutrients and other growth factors in this specialized environment. For example, precipitation can provide nutrients in dissolved, bioavailable form at levels often far exceeding concentrations available to phytoplankton of oligotrophic systems (Parker et al. 1981). Danos et al. (1983) found significantly higher concentrations of dissolved inorganic nitrogen, phosphorus, silica and pigments in the surface microlayers of experimental ponds. Also, the surface microlayer of seawater is enriched with surface active substances such as fatty acids and proteinaceous materials (Duce et al. 1972; Hardy 1982; Bărlocher et al. 1988) which may act as chelators of trace elements required by neustonic species - elements which might not be available to planktonic species. A similar enrichment of the surface microlayer of freshwater forest pools might be expected given the usually high organic content of their terrestrial surroundings and the associated opportunities for the supply of vitamins and other growth factors.

The surface film algal community may be immune from grazing by micro-crustaceans that are adapted for planktonic filter-feeding. This specialized habitat may therefore provide a refuge and protection from one of the important loss mechanisms influencing phytoplankton. However, protists with special adaptations for existence at the air-water interface, such as hypotrichid ciliates (Ricci et al. 1991), may exert some influence on

phytoneuston communities. Also, because of the specialized habitats of neustonic chrysophytes (mainly physically stable, small, shallow forest pools), neustonic chrysophytes have not in the past created any special problems for human use of these waters. These specialized communities do, however, offer their potential use as model systems for investigation of a number of chrysophyte related phenomena, including bacterial - flagellate interdependencies and the possible production of volatile compounds which might inhibit the growth of other organisms.

Information Needs

> "A more definite knowledge of the factors involved in the development of blooms in fresh and salt water can certainly be gained from physiological experiments with cultures and simultaneous qualitative and ecological observations" (English translation from German)
>
> Kolkwitz (1914)

This review has, I hope, consolidated some of the known information about the mass occurrences of chrysophytes. However, it has also probably served to point out a number of deficiencies in our understanding of the phenomena. I hope that many of these information gaps will have already become apparent to the reader, but at the risk of stating the obvious, I would like to provide my own thoughts on required future

directions for chrysophyte bloom research.

(I) There is a need to continue development of remote sensing technology, especially as it relates to coastal marine areas. The absorption and fluorescence spectra of Aureococcus, the marine "brown-tide" organism, are different from those of other coastal marine phytoplankton species (Yentsch et al. 1989); this might be exploited by remote sensing. Recent advances in multispectral scanning technology are leading to real-time assessments of the extent and dynamics of both marine and freshwater algal blooms (Balch et al. 1991; Millie et al. 1991).

Even if the extent and frequency of marine algal blooms do not increase in the future, the impacts of the marine blooms of the future will undoubtedly be more dramatic as coastal salmon culture intensifies. Net pen farming of both Atlantic and Pacific salmon now accounts for 30% of the world's production of canned salmon. It has been predicted that by the year 2000, farmed salmon will account for 90% of the total (Van Dyk 1990). Penned salmon are vulnerable to algal blooms. On the British Columbia (Canada) coast alone, fish farming losses resulting from diatom blooms have averaged between $2-4 million annually over the period 1986-1990 (Red Tide Newsletter, 3(2):11, April, 1990). The Prymnesium parvum bloom on the Norwegian southwest coast in 1989 caused losses of caged salmon valued at $5 million (Kaartvedt et al. 1991).

In the path of an advancing algal bloom, the only reactions possible today are, 1) harvest the fish prematurely, 2) tow the net pens out to sea beyond the influence of the bloom or 3) take a chance on the severity of the effects of the bloom. Early warning systems based in part on remote sensing technology would help in selecting one of these options.

(II) More biochemical and toxicological work needs to be done on the volatile excretory products of chrysophyte bloomers, especially Synura and Uroglena species. One striking feature of the big blooms is that they are essentially unialgal. This begs the question "are other species excluded because of toxic excretions"? Kamiya et al. (1979) have demonstrated the presence of fatty acid ichthyotoxins in Uroglena volvox, and toxin production by axenic cultures of Ochromonas has also been found (Spiegelstein 1969). This is important because there is at the present time a debate in progress on the role of bacteria in the production of toxins associated with some marine dinoflagellate blooms (Taylor 1990). If bacteria are not implicated in the production of chrysophyte toxins, as the scant research data would suggest, then progress in determining factors responsible for toxin production might be relatively rapid because the work would be based on a simpler biotic system.

Some indirect evidence for toxin production by either (or both) of Synura or Chrysochromulina breviturrita may exist in data from Dickie Lake in Ontario.

Over a 15 year period of observation, years with high biovolume of Synura were also years with low biovolume of Chrysochromulina breviturrita and vice versa (Fig. 5). The recent Chrysochromulina polylepis poisonings in the Baltic (Underdal et al. 1989) provided the first evidence for toxin production by members of the prymnesiophyte genus Chrysochromulina (but see Nicholls et al. 1982). It cannot be determined conclusively from the Dickie Lake data on hand whether or not C. breviturrita and Synura have inhibited each other's growth; however, the within year data suggest that Synura may have inhibited Chrysochromulina because the Synura populations typically developed before the Chrysochromulina populations. Chrysochromulina didn't develop until mid- to late summer, and then apparently only in Synura's absence (Fig. 5). At this point, this is speculative, but suggestive, and some experimental work needs to be done on species interactions that include Synura, Uroglena and other bloom formers. Included under the general topic of species interactions might also be the role of parasitic symbioses and predation by non-crustaceans such as Bodo and Rhizoochromonas species (Nicholls 1987,1990) as potential regulators of chrysophyte populations. What are the environmental factors that allow Bodo crassus and Rhizoochromonas endoloricata to achieve high population densities?

(III) Because their flagellar structure is different from that of phagotrophic chrysophytes with the ochromonad flagellation type, Mallomonas and Synura are unlikely to utilize bacteria directly as a food source in the same way that several

ochromonadalean species do (including Dinobryon and Uroglena) (Bird and Kalff 1986; Kimura et al. 1986a, 1986b; Boraas, this volume). Still, the other roles of aquatic bacteria in modifying the growth medium and helping to structure the phytoplankton community (Newhook and Briand 1987) need to be investigated with reference to chrysophyte blooms.

(IV) Although much is now known about the physical and biochemical properties of dissolved organic matter (Gjessing 1976; Steinberg and Muenster 1985), there are still important information gaps relating to the effects of natural organic materials on aquatic organisms (Serrano and Guisande 1990; Steinberg 1990). The role of organic acids and iron in dystrophic systems, both as directly available essential growth factors and as substances regulating the availability of essential trace elements, needs further work with respect to chrysophytes. There is some evidence that the humic contents of Scandinavian lakes is increasing at rates as high as 3% per year (Forsberg and Petersen 1990). Graneli et al. (1989) have demonstrated enhanced growth of dinoflagellates in response to experimental additions of humic substances in coastal areas of the Baltic influenced by these increased inputs of dissolved humic materials from adjacent watersheds. Similar experiments need to be done in freshwater systems with potential bloom forming chrysophytes.

(V) Experimental use of "BIOTRON" type technology (e.g., Ostroff et al. 1980;

Graham et al. 1985) should be encouraged for multifactorial laboratory investigation of light, temperature, nutrients and other variables influencing chrysophyte growth rates, and in particular, to answer questions about surface water accumulations of Uroglena. Some relevant questions are: 1) where does the population producing the surface bloom develop? 2) what causes mass movement to the surface and what is the relative importance of active motility and passive buoyancy? 3) once at the lake surface, are cells viable? 4) what are the time dependent effects on cell viability of potentially damaging high intensity solar irradiance at the lake surface? 5) what are the diurnal vertical movements under thermally stratified conditions? and 6) what are the relative roles of the water column light, temperature and nutrient gradients as regulators of vertical movements in the population? These questions might be answered through a combination of careful observations of wild populations and laboratory experimentation .

SUMMARY

Although there are many unanswered questions relating to the causes of chrysophyte blooms, an apparent pattern has emerged from the recent studies of algal blooms in coastal marine environments and freshwater lakes. That is that human influences in the form of increased nutrient supply from human waste, drainage from agricultural operations, and contaminated precipitation provide the basic chemical medium for

promoting blooms. While this is probably a valid conclusion for algal blooms in general, the relevance of this conclusion to the Chrysophyceae in particular has not been well defined, especially for freshwater populations. Although chrysophyte blooms have resulted from experimental fertilizations, a number of whole-lake and in-lake enclosure fertilization experiments have not produced chrysophyte blooms. The triggering of a chrysophyte bloom likely depends on the achievement of fundamental growth conditions which are species specific and which may be realized only when the "right" combination of natural and anthropogenically derived variables comes together. These natural environmental variables could include temperature, salinity, hydrologic flushing rate, turbulence, light, grazing, and inter-species competitions and inhibitions. Because these natural influences are multi-factorial and highly interactive, their combinations in ways that could trigger algal blooms are not predictable, given our present level of understanding of the ecology of the most important bloom-forming species. A number of experimental approaches to specific questions about the role of volatile excretory substances as inhibitors of other algae, the role of bacteria either directly as an energy source for phagotrophic chrysophytes, or indirectly as facilitators of nutrient availability, and the role of chrysophyte motility (vertical migration), zooplankton grazing and light effects are among those topics suggested as fruitful lines of future research on the chrysophyte bloom phenomenon.

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TABLE 1 Common odours in the influents of three drinking water utilities expressed as percentage occurrence of all odours.

UTILITY	ODOUR CHARACTERIZATION	PERCENTAGE OCCURRENCE
Philadelphia Suburban Water Co.	"sewage"	83
	"creeky"	20
	"musty"	10
Philadelphia Water Department	"decaying vegetation"	62
	"septic (sewage)"	52
	"vegetation"	22
	"earthy"	43
	"musty"	17
	"fishy"	13
Lyonnaise Des Eaux	"muddy"	71
	"fishy"	71
	"musty"	38
	"septic"	29

From Bartels et al. (1989)

TABLE 2 Densities of organisms associated with odours in drinking water from Lake Lyseren, Norway.

ORGANISM	CONCENTRATION (cells/mL)	DATE
Chlamydobacteria	2000	July 27, 1976
Chlorococcales	193	July 27, 1976
Asterionella formosa Hass.	60	July 31, 1975
Tabellaria fenestrata (Lyngb.) Kütz.	145	July 31, 1975
Dinobryon divergens Imh.	560	August 1, 1975
D. sociale var. stipitatum (Stein) Lemm.	2000	July 31, 1975
Chrysomonads	12000	July 31, 1975

From Berglind et al. (1983)

TABLE 3 Occurrence of Uroglena blooms in Ontario lakes during 1987-1990.

Lake	Township	Z_{max} (m)	Total P (μg P/L)	Alkalinity (mg $CaCo_3$/L)	Secchi Disc (m)
Paint	Ridout	21.4	10	5.4	2.1
Pine	Wood/Musk	22.6	8	2.6	3.8
Black	Wood	3.4	12	0.9	1.5
Leech	Oakley	13.7	6	2.2	4.6
Bigwind	Oakley	36.3	6	2.9	5.0
Clear	Oakley	26.8	5	3.0	5.8
Kawagama	M^{c}Clintock	73.2	3	2.4	9.3
Fletcher	M^{c}Clintock	30.5	?	3.7	?
Muskoka	Muskoka	66.5	5	4.6	5.1

TABLE 4 Volatile excretory products of three algal species, including the chrysophyte Synura uvella.

Location and Date	Dominant Species	Excretory Products
Lake Constance	Anabaena sp.	dimethyldisulfide
17 October, 1978		
Lake Constance	Asterionella formosa	octadiene
19 July, 1979		octatriene
Wahnbach Reservoir	Synura uvella	penten-3-one
10 October, 1978		pentanone-3
		octanone-3
		octanol-1
		octanol-3
		oct-1-en-3-ol
		2-pentylfuran
		trans,cis-2,4-decadienal
		β-cyclocitral
		6-methylhept-5-en-2-one
		β-ionone

From Jüttner (1981)

TABLE 5 Summary of chrysophyte responses to experimental nutrient additions

REFERENCE	LAKE	TREATMENT	RESPONSE
Langford (1950)	Four lakes in Algonquin Park, Ontario	Agr. fertilizer (12-24-12); 0.05-0.9 mg P/L	All lakes responded 3-4 weeks after treatment with large increases in diatoms and Dinobryon (and Synura in one lake)
Smith (1969)	Crecy Lake	210 μg N/L;390 μg P/L; 270 μg K/L	Main response was in Anabaena and Spirogyra blooms, but Dinobryon bloomed in 1961, three years after the last fertilization.
Schindler et al. (1971, 1973), (Kling and Holmgren (1972), Findlay and Kling (1975), Findlay (1978, 1981, 1983)	ELA Lake 304	Two years of each of the following treatments: N, P and C; N and C; N and P	Dinobryon and Synura occasionally among dominants in early summer of some years
See above	ELA Lake 261	Four years of H_3PO_4 additions	Dinobryon, Mallomonas, and Synura consistently among the dominants; Uroglena important only in 1975
See above	ELA Lake 227	Inorganic P and N added weekly for several years	Inconsistent response with occasional domination by Dinobryon and Mallomonas spp in some years.
Findlay and Kasian (1987)	ELA Lake 226NE and 226SW	Basin divided by a curtain; 226NE fertilized with N, P and C, and 226SW, with N and C.	Dinobryon less important in 206NE; occasional dominance by Synura in both basins; Uroglena was a dominant in 226NE during all three post fertilization years.
Ramberg (1976)	Lakes Vitalampa and Botjarn, Sweden	Fertilization for one year with NH_4NO_3	Chrysophyte portion of total phytoplankton showed little change from pre-fertilization years
Witt (1977)	Vorderer Finstertaler See, Austria	Additions of P as NaH_2PO_4	Shift from dinoflagellates to chlorophytes; no response in chrysophytes
DeNoyelles and O'Brien (1978)	eight 0.1 ha ponds, Cornell Univ.	N, P and K in low, medium and high dose rates	Chrysophytes remained dominant in reference ponds, but were replaced by chlorophytes and cyanophytes in treated ponds

Reinertsen (1982)	Lake Langvatn, central Norway	N, P and K supplied as commercial fertilizer in 1975 and 1976	No major response among Synura, Uroglena or Dinobryon (all three present prefertilization)
Yan and Lafrance (1984)	Mountain top and Labelle Lakes, Sudbury, Ont.	P and N added as 20-40-0 commercial fertilizer and as H_3PO_4 and NH_4NO_3	Dinobryon and Mallomonas spp replaced by other algae, mainly Cryptomonas spp
Yan and Lafrance (1984)	Middle and Hannah Lakes, Sudbury, Ont.	P added as H_3PO_4	Low level fertilization resulted in continued domination of chrysophytes; higher fertilization rates led to replacement by other groups
Wilcox and DeCosta (1984)	Cheat Lake, W. Virginia	P added to enclosures as KH_2PO_4	Dinobryon replaced by chlorophytes
Holmgren (1984)	Four lakes in the Kuokkel area of N. Sweden	N and P added as NH_4NO_3 and H_3PO_4 in various combinations over several years	Additions of N alone stimulated Uroglena; N and P additions to the same lake the following year led to dominance by Uroglena and Dinobryon, but by cryptophytes in another lake; additions of P alone inhibited Dinobryon spp
Chow-Fraser and Duthie (1987)	An embayment of Lake Matamek, Quebec	N and P added as $NH_4H_2PO_4$	Dinobryon crenulatum was one of 17 taxa showing a significant increase
Olofsson et al. (1988)	Lake Hecklan, Central Sweden	Continuous low dosage of N and P in commercial fertilizer	Chrysophytes dominated before and after fertilization with only minor shifts in community composition

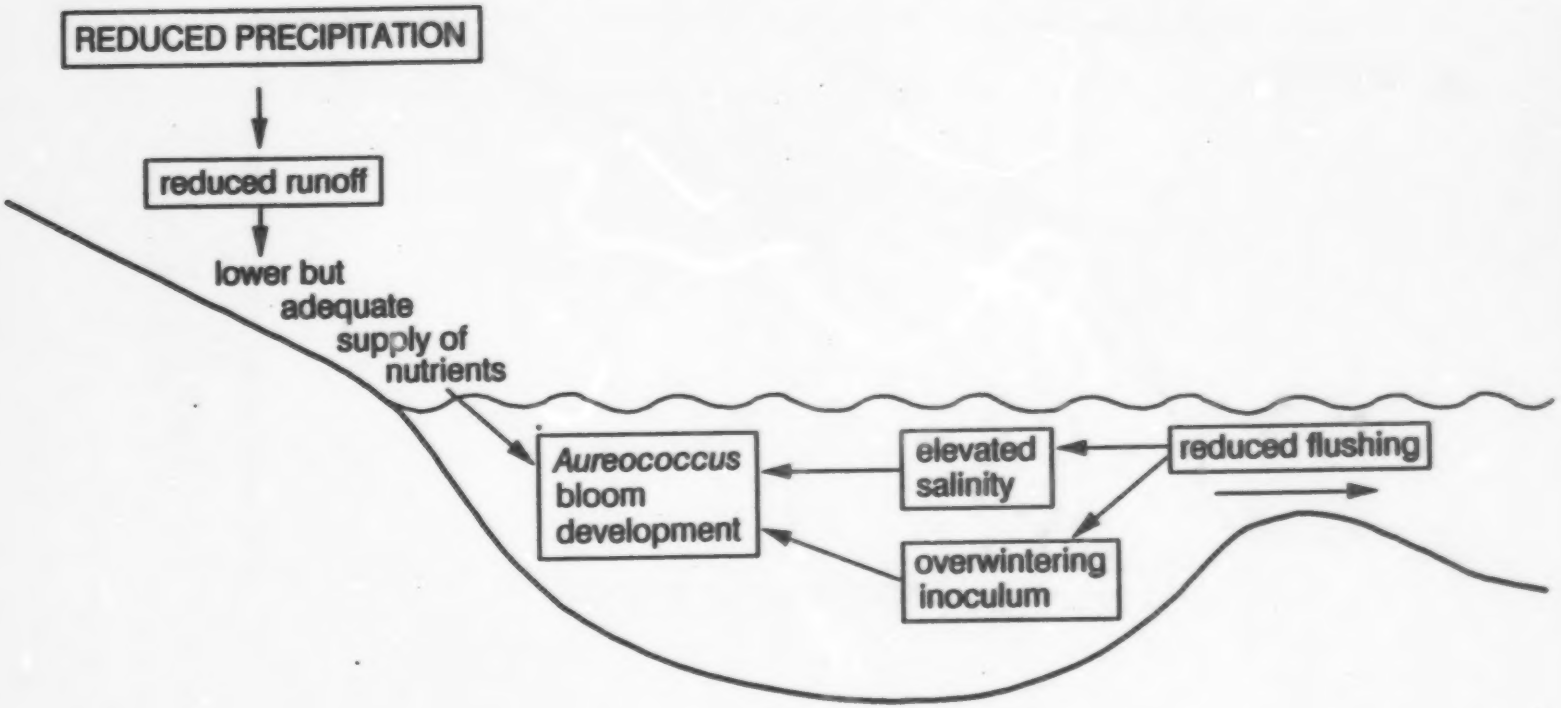

Figure 1 An hypothesis relating precipitation and associated physical-chemical changes to development of Aureococcus blooms in Long Island embayments (after Cosper et al. 1990).

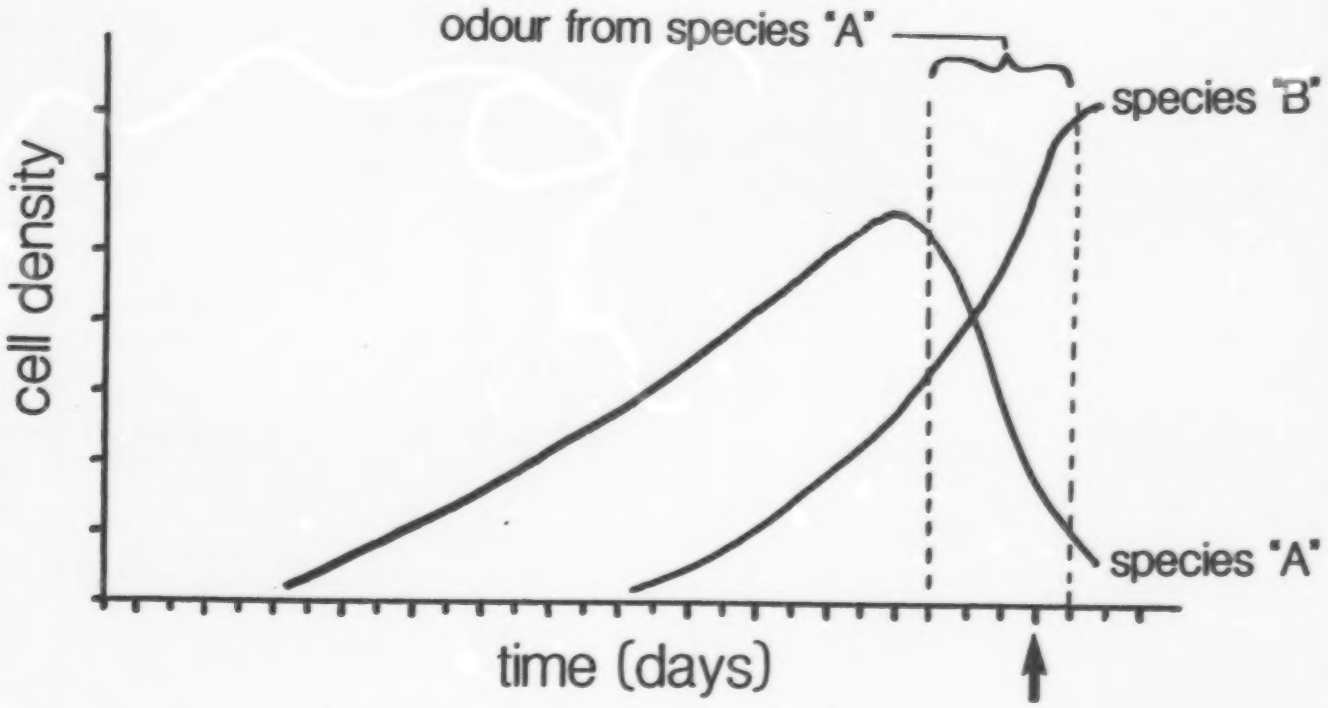

Figure 2 Hypothetical population density changes over time for two phytoplankton species, "A" and "B", of which, only species "A" is an odour producer. If sampling and identification are done at the peak of odour production but after the population has peaked (arrow), species "B" may be erroneously implicated as the cause of the problem.

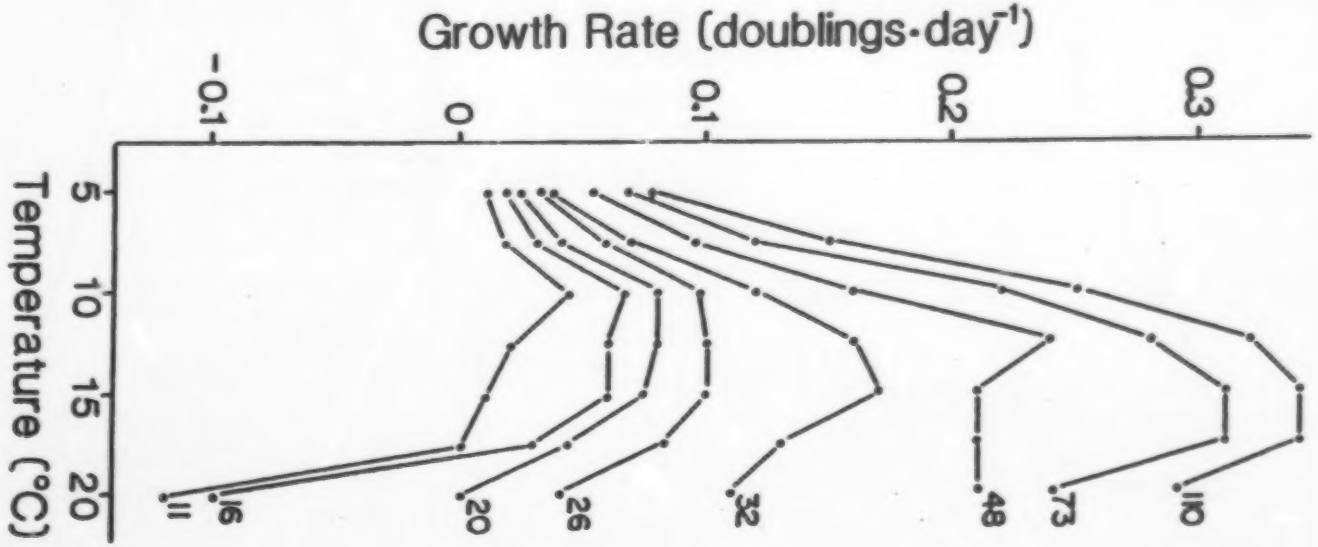

Figure 3 The effects of temperature on the growth rate of cultured Synura sphagnicola at eight different light intensities ranging from 11-110 $\mu E/M^2/s$ (from Healey 1983).

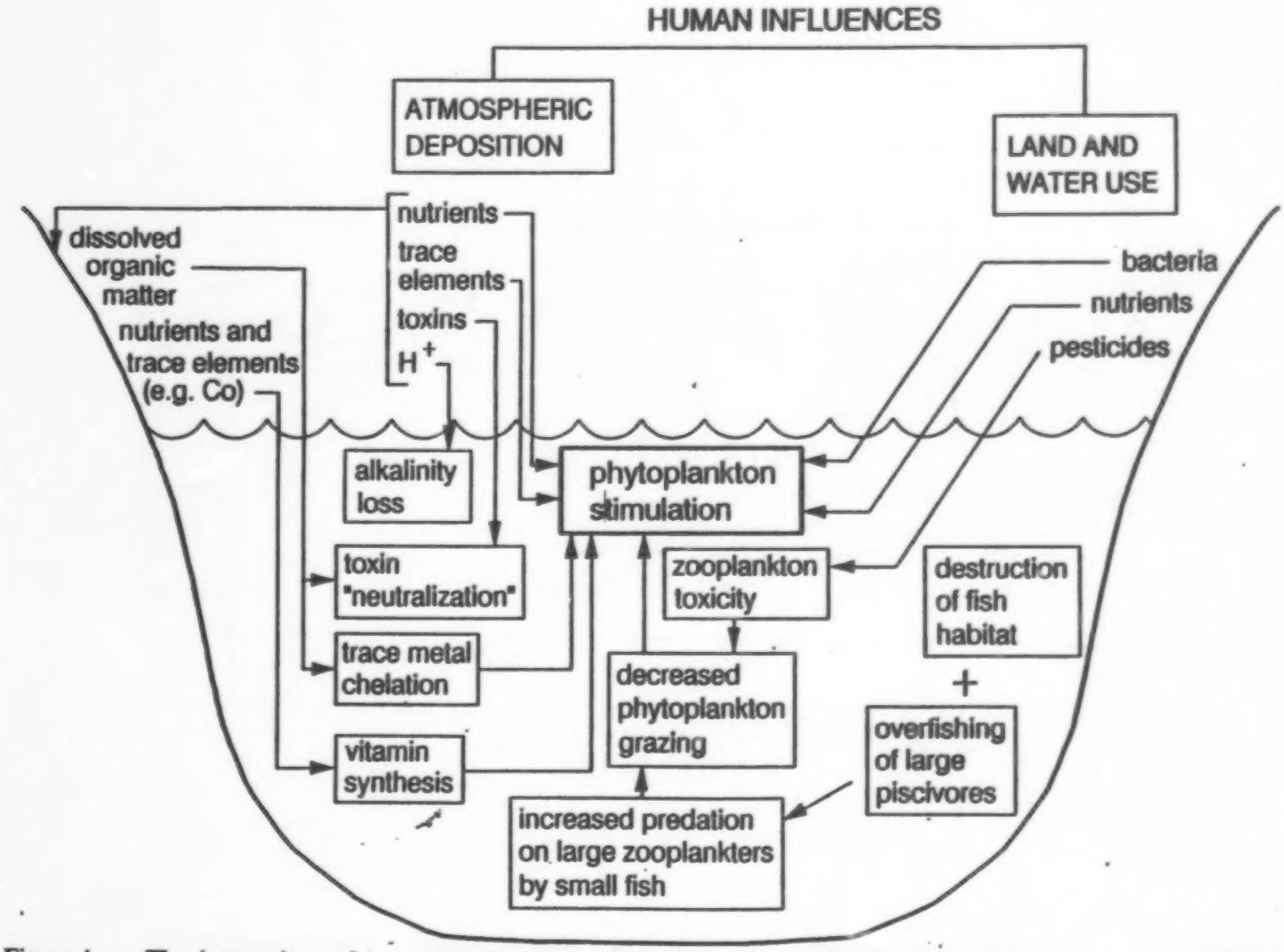

Figure 4 The interactions of a number of factors originating from human influences and their stimulatory effect on phytoplankton in a hypothetical software lake.

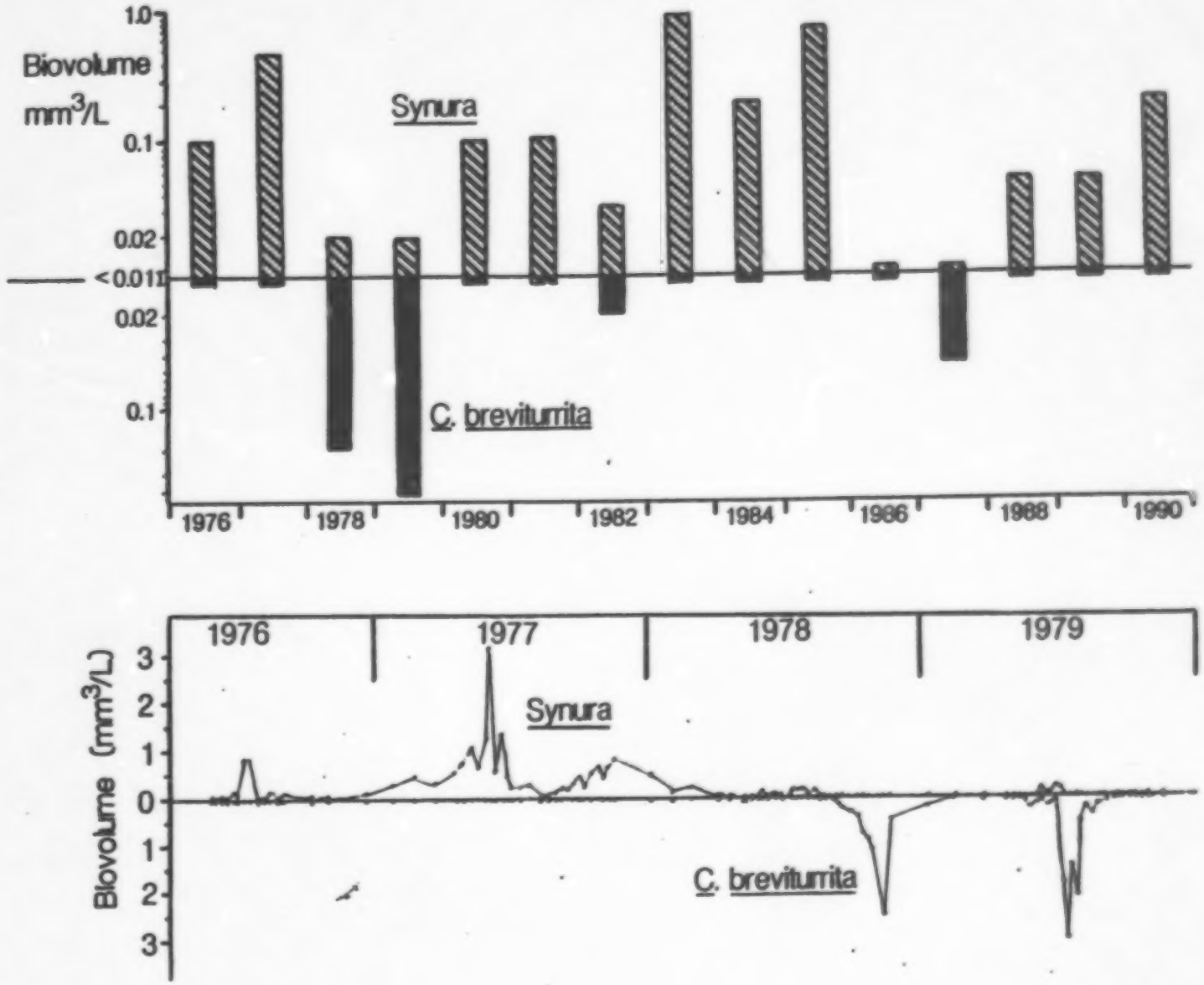

Figure 5 a) Annual average biovolume of Chrysochromulina breviturrita and Synura spp. in the phytoplankton of Dickie Lake, 1976 - 1990; b) Seasonal distributions of C. breviturrita and Synura spp., 1976 - 1979 (Nicholls unpubl).